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CURRENT STATE OF AND PROSPECTS FOR SELECTION IN REINDEER HUSBANDRY

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ACADEMIC DISSERTATION

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*“Tokan tuottavuuden ylläpito on tarkempaa työtä kuin kellosepällä”
[“Maintaining the productivity of a reindeer herd requires more
precision than a watchmaker’s work”]*

- haastateltu poroisäntä [A manager of a cooperative]

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ABSTRACT

Reindeer husbandry is highly valued in Finland. Nevertheless, the profitability of reindeer herding could be improved. Limited pasture resources restrict the opportunities for increasing the number of animals per area; hence, the focus should be on higher quality. Selection of breeding animals could be an effective tool for economic development, bringing with it permanent changes in productivity. Information on the practices of and potential for selection in reindeer husbandry is lacking. The aim of this study was to examine the current state of selective breeding, genetic variation in the traits related to meat production and prospects for genetic improvement.

The current state of selection was explored by interviewing the managers of reindeer-herding cooperatives. All the responding managers (45/56) considered selection very important among the herding operations. Meat production was regarded as the main source of income, and the main selection criteria for improving the efficiency of production were calf size and dam properties. They were highly prioritized throughout the reindeer-herding area. Hence, it is feasible to contemplate founding joint operations for genetic improvement, such as guidelines and recommendations for breeding schemes, regardless of the region or cultural background of a herder.

The variation in meat production traits was studied, using Kutuharju (Kaamanen, Finland) experimental reindeer data. The calf traits included *birth date*, *birth weight* and *growth*. The variation was highly influenced by environmental and management factors. Some of the annual variation could be explained by the North Atlantic Oscillation indices summarizing major weather conditions. The calf traits had direct heritability values of 0.23–0.27, while birth weight and growth also showed maternal heritability values of 0.18–0.24. The direct-maternal genetic correlation in growth was strongly negative (-0.73); therefore dam quality must also be included in the selection criteria.

In addition to the dam's maternal care, her *age at maturity* and lifetime production were analysed. The age at maturity showed little genetic variation. The lifetime production was expressed as *cumulative calf production* and *individual fitness*. The cumulative calf production showed heritability values of 0.22–0.30.

The animals used for breeding purposes were selected among 6-month-old calves. Females' own calf weight and early calf production are favourably correlated with lifetime production and therefore serve as indicator traits for productivity.

The use of selective breeding in reindeer husbandry shows promise. Selection intensity and generation turnover are high and genetic variation in meat production traits encouraging. Future success requires development in animal identification, accurate measurements, organized data collection and possible applications of new pedigree and selection tools resorting to genomics.

Reindeer husbandry is facing challenges, such as degraded and fragmented pastures due to changes in environmental conditions (climate warming and predation pressure) and human activities (tourism, traffic and industry). Reindeer meat has a positive image as an ethically produced and tasty product. Reindeer husbandry is a traditional livelihood that has, over time, adapted to new situations and is likely to continue doing so by adopting new ideas and relying on sound future collaboration.

Key words: reindeer, *Rangifer tarandus*, selection, genetic variation, animal breeding, reindeer husbandry

Asiasanat: poro, *Rangifer tarandus*, valinta, geneettinen vaihtelu, kotieläinjalostus, porotalous

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications:

- I** Muuttoranta, K. and Mäki-Tanila, A. 2014. Reindeer production in Finland – integration of traditional and new technologies. An edited version of the article has been published in: Cattle husbandry in Eastern Europe and China (2014). Edited by Kuipers, A., Roztalnyy, A. and Keane, G. EAAP Scientific Series, Publication No. 135. Published by Wageningen Academic Publishers, Wageningen, the Netherlands. ISBN: 978-90-8686-232-0978, DOI: 10.3920/978-90-8686-785-1.
- II** Muuttoranta, K. and Mäki-Tanila, A. 2011. Selection decisions among reindeer herders in Finland. *Rangifer* 31: 129–138.
- III** Muuttoranta, K. and Mäki-Tanila, A. 2012. Regional differences in reindeer herding operations in Finland. *Acta Agriculturae Scandinavica, Section A – Animal Science*, 62: 142–152.
- IV** Muuttoranta, K., Tapio, M., Holand, Ø., Røed, K.H., Nieminen, M. and Mäki-Tanila, A. 2013. Genetic and environmental factors affecting the birth date and birth weight of reindeer calves. *Rangifer*, 33: 25–35.
- V** Muuttoranta, K., Tapio, M., Holand, Ø., Røed, K.H., Nieminen, M. and Mäki-Tanila, A. 2014. Genetic variation in meat production related traits in reindeer (*Rangifer t. tarandus*). *Rangifer* 34: 21–36

The publications are referred to by their Roman numerals in the text. Copies of the original articles (**II–V**) and the manuscript of an edited article (**I**) are included with the kind permission of their respective copyright owners.

The author participated in planning the studies, performed the interviews (**II**, **III**), performed all data editing and statistical analyses, interpreted the results together with the coauthors and was the main writer of all the articles.

ABBREVIATIONS

ADG	average daily gain, measure of growth rate
ANOVA	analysis of variance
AW1	calf's weight in first autumn
BD	birth date of reindeer calf
BW	birth weight of reindeer calf
CAW1	autumn weight of dam's first calf
CV%	coefficient of variation
CV _A	evolvability
D_ADG	average daily gain of a female (as a calf)
DAW1	dam's weight in her first autumn (as a calf)
DW	dam's adult weight in autumn prior to calving
E _d	environmental effect in animal
E _m	maternal (temporary) environmental effect
EUROP	carcass classification system
G _d	direct genetic effect of the animal
G _{d(D)}	direct genetic effect of dam
G _{d(S)}	direct genetic effect of sire
G _m	maternal genetic effect
GxE	genotype-environment interaction
h ²	heritability
h ² _d	direct heritability
h ² _m	maternal heritability
h ² _W	Willham's heritability
λ _{ind}	individual fitness
NAO	North Atlantic Oscillation
PCA	principal component analysis
PE _m	maternal permanent environmental effect
r _{am}	direct-maternal genetic correlation
r _{ce}	direct-maternal environmental correlation
r _g	genetic correlation
r _{g(d)}	direct genetic correlation
r _{g(m)}	maternal genetic correlation
r _p	phenotypic correlation
r _e	residual correlation
REML	restricted (residual) maximum likelihood
S-MGS	sire-maternal grandsire
σ, SD	standard deviation
σ ²	variance
SE	standard error
T ²	total heritability
WW7	cumulative weaning weight of calves over seven years

1 INTRODUCTION

1.1 REINDEER HUSBANDRY IN FINLAND

Reindeer (*Rangifer tarandus tarandus* L.) have been a vital resource for the inhabitants of Lapland for centuries (Røed 2005). They have provided food, transportation, hides and other raw materials for peoples living in the north (Ingold 1978). Reindeer husbandry is currently a very important occupation locally and is a fundamental part of northern culture and a sense of identity of the Saami people (Riseth 2000, Mazzullo 2010, **I**). There were 4530 reindeer owners in Finland in the reindeer-herding year 2011/2012 (Paliskuntain yhdistys 2013). Non-Saami people are also allowed to be reindeer herders, in contrast to these in Sweden and Norway (Poronhoitolaki 1990, **I**).

Reindeer are semidomesticated and roam free in the environment for most of the year, being exposed to harsh natural conditions. Reindeer live in an extensive pastoral system and convert natural pastures to meat and other products (Poronhoitolaki 1990, **I**). They are gathered in autumn for roundups, in which they are separated into slaughter and breeding animals. Most of the meat produced originates from calves born in spring and slaughtered in autumn; the best calves are left for recruitment (**I**).

The annual production of reindeer meat is about 2–3 million kg. Reindeer husbandry includes an annual total revenue of €32 million (2012), half of it originating from meat production (Paliskuntain yhdistys 2013, **I**). The other half is made up of income, e.g. from tourism, meat processing and subsidies (Rantamäki-Lahtinen (ed.) 2008, Paliskuntain yhdistys 2013, **I**). Compared with the total annual Finnish meat production of 350 million kg (Tike 2012), the volume from reindeer meat production is small. Reindeer meat is regarded as a luxury product that meets consumers' desires for lean, local and ethically produced meat (Hoffman and Wiklund 2006).

Productivity can be described by the animals' condition (carcass quality) or production of meat per unit area (Lundqvist *et al.* 2009). Usually, productivity is improved by increasing the scale of operations or number of animals (e.g. Riseth 2000). Limited resources, mainly winter pastures (Poronhoitolaki 1990, Kumpula *et al.* 2002), restrain the number of animals in cooperatives. Furthermore, expanding mining and forestry industries, among others, have conflicting objectives for land use with reindeer husbandry (e.g. Kumpula *et al.* 2009). Other players affect the pasture areas and cause disturbance to reindeer by increased traffic and motorization (Anttonen *et al.* 2011). Due to fragmented and limited pastures, instead of volume the quality of production is increasingly regarded as the key area in development work.

Herd production is a combination of several factors (see review by Lundqvist *et al.* 2009). Herders can ameliorate herd productivity by management and selective breeding. Management includes daily control of

the herd, optimization of herd composition and slaughter strategy, and feeding (Riseth 2000, Holand 2007, I). Rönnegård (2003) reviewed the three steps towards optimum herd productivity originally reported by Danell (1999): 1) optimal herd size as related to available pasture area, 2) maximum number of productive females and 3) selective breeding, based on production records to improve the genetic quality of individuals. The list could be amended by 4) integration of genetic improvement with management operations to incur a minimum of additional costs due to selection (Öje Danell, *pers. comm.*).

A formal, consistent selection scheme in reindeer husbandry is lacking, despite Rönnegård's (2003) background study on the effects of selection, inbreeding and maternal effects. Guidelines for more efficient selective breeding may improve animals' quality and herd productivity. We offer additional information on reindeer and reindeer production, including issues related to the history and development of reindeer herding in Finland, biology of reindeer, the main products and market, changes in pastures and other resources, and optimization and opportunities in production (I).

1.2 SELECTIVE BREEDING IN REINDEER HUSBANDRY

The aim of selective breeding is to achieve permanent changes in productivity of the population (Danell 1999, Flint and Woolliams 2008). Genetic gain can be achieved by selecting genetically superior animals to be the parents of the next generation. Genetic gain, in general, is dependent on the genetic variation available in the traits (and genetic correlation (r_g) among the traits), accuracy of the selection criteria used for proxying the breeding objectives, selection intensity and generation turnover (Falconer and Mackay 1997).

The semidomesticated nature of reindeer husbandry limits the opportunities for selective breeding. Even information on the current use of selection is lacking. In contrast to farmed livestock, individual markings of animals are not required, while in reindeer only owner-specific notches are cut in the ears to mark the ownership (Poronhoitolaki 1990, I). Furthermore, no performance records on the individuals are available; hence, the current selection cannot be based on records or pedigree, but on the phenotypes of the animals (Danell 1999, I).

BREEDING OBJECTIVES AND SELECTION CRITERIA

The definition of breeding objectives is the first and most important step in effective genetic improvement. The breeding objective is a combination of traits with additive genetic variation and economic values, and they form the basis for choosing the selection criteria and organizing the recording scheme (Goddard 1998). The breeding objectives in reindeer husbandry need to be

related to converting the pastures into products (Danell 1999, I). The most important product in reindeer husbandry is meat; therefore, calf growth and survival are the key selection criteria (Danell 1999, I). The maternal ability that supports calf production, survival and growth, is crucial in reindeer (Rönnegård 2003). The selection objectives and data recording need to be related to the environment in which the offspring are raised and also as a response to societal concerns (longevity and animal welfare), and to the management of genetic resources and diversity (Flint and Woolliams 2008).

IMPORTANCE OF SELECTION

The benefits of selection in reindeer have been demonstrated in pioneering schemes. Selective breeding has markedly improved productivity in the Riast-Hylling cooperative in Norway (Lenvik 1988, Riseth 2000) and in Ruvhten Sijte in Sweden (Rönnegård 2003, Rönnegård and Danell 2003). In both schemes, the calf weights and information on dam productivity were recorded and used as selection criteria. Together with improved herd composition and calf slaughtering strategy, the meat production per animal in the spring herd has increased in Riast-Hylling from 8 kg to 14 kg in 1976–1994 (Lenvik 1988, Riseth 2000). In Ruvhten Sijte, the genetic gain from selection was predicted to be 2.0 kg live weight in 11 years, corresponding to 0.4% of the phenotypic mean (Rönnegård and Danell 2003). Smith (1984) reviewed the annual genetic gain, ranging from 0.3% to 1.5%, of the phenotypic mean in sheep (*Ovis aries*) and beef cattle (*Bos taurus*).

The genetic variation in the traits related to meat production has so far been rarely studied in reindeer (Varo 1972, Rönnegård and Danell 2003, Appel and Danell unpubl., in Rönnegård and Danell 2003). Rönnegård and Danell (2003) estimated the realized heritability (h^2) and developed a concept of potential selection response for reindeer, in which no prior knowledge of heritability values is needed, but the gain from selection can be estimated comparing the phenotypic differences between two herds in a similar environment. However, accurate heritability and correlation estimates ease the assessment of needed information and the feasibility of a selection scheme, given the breeding objectives.

1.3 MATERNAL EFFECTS

In many farm animal species, maternal effects, such as milk production and care, influence calf performance (Willham 1972, Varo and Varo 1970, Rönnegård 2003, Bijma 2006). In genetic analyses, the maternal effect in the calf trait can be divided into the maternal additive genetic effect and permanent environmental effect of the dam (Willham 1963, 1972, Figure 1). Maternal heritabilities (h^2_m) in reindeer are lacking.

The direct-maternal genetic correlation (r_{am}) is often strongly negative, leading to a decline in maternal capacity, if only direct traits are selected (Koerhuis and Thompson 1997, Heydarpour *et al.* 2008, Eaglen and Bijma 2009). The negative estimates have often been questioned, as they may have i) arisen from the data structure (Meyer 1992, Heydarpour *et al.* 2008), in particular, the distribution of data over fixed effects (Meyer 1997), or ii) ignored the correlation of residuals between the dam and offspring effects (Koerhuis and Thompson 1997, Bijma 2006, Eaglen and Bijma 2009). The residuals correlated are likely a general phenomenon in livestock (Bijma 2006). A typical example in cattle is “fatty heifer syndrome”, in which the development of the udder is restricted, inducing a decline in maternal ability among the daughters of good dams (Meyer 1997). In reindeer, Varo and Varo (1970) found a negative phenotypic correlation between dam weight and the protein content in her milk.

Falconer (1965) proposed the use of regression of the calf’s record on dam’s record as the trait for estimating such a correlation. In multigeneration data, the estimation is problematic and Koerhuis and Thompson (1997) suggested that the respective covariance be included in Willham’s (1963) model. With a small amount of data, such addition would not usually lead to satisfactory convergence.

When selection is done for the calf trait, ignoring maternal effects, the potential change can be quantified by Willham’s (1972) heritability, ($h^2_w = h^2_d + 1.5 r_{am}h_d h_m + 0.5 h^2_m$), where h^2_d and h^2_m denote direct and maternal heritabilities. The total heritable variance available for selection is denoted by T^2 (total heritability) and it equals $\frac{\sigma^2_{a(d)} + 2\sigma_{a(dm)} + \sigma^2_{a(m)}}{\sigma_p^2}$ (Eaglen and Bijma, 2009). In the equation σ^2_a is additive variance, $\sigma_{a(dm)}$ additive direct-maternal genetic covariance, $\sigma^2_{a(m)}$ is additive maternal genetic variance, $\sigma^2_{a(d)}$ is additive direct genetic variance and σ_p^2 is phenotypic variance.

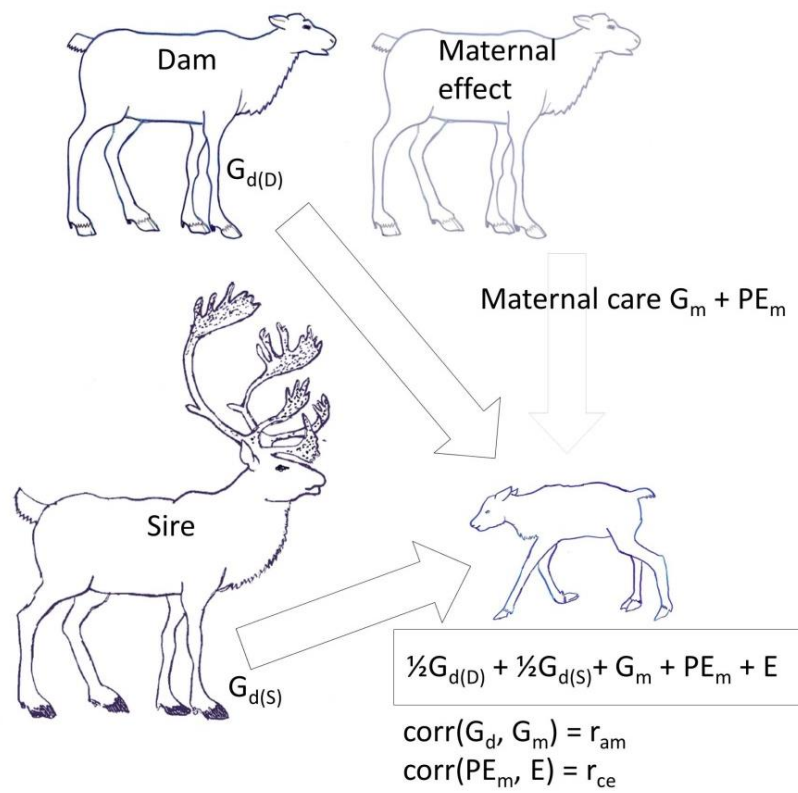


Figure 1

Direct and maternal effects on offspring phenotype. The direct effect (G_d) is split into the sire's (S) and dam's (D) additive genetic effect. The maternal effect consists of the maternal genetic effect (G_m), maternal permanent environmental effect (PE_m) and maternal temporary environmental effect (E_m). The direct-maternal genetic correlation is denoted as r_{am} and the respective direct-maternal environmental correlation as r_{ce} (the reindeer figures are modifications of those by Mauri Nieminen).

2 OBJECTIVES OF THE STUDY

The main goals of the thesis are two: to determine the status of selective breeding and selection decisions in reindeer husbandry and to estimate the genetic variation in the traits affecting meat production efficiency.

The objectives consist of four elements (with article numbers in parentheses), whose purposes were to determine:

1. the importance of selective breeding among herders and identifying the selection criteria used by herders (**II, III**)
2. the regional differences in herding operations and selective breeding in the reindeer-herding area in Finland (**I, III**)
3. the genetic variation in calf traits: birth date (BD), birth weight (BW) and growth (**IV, V**)
4. the genetic variation in dam traits: age at maturity, individual fitness (λ_{ind}) and lifetime calf production (WW7) (**V**).

The results provide information needed for determining the prospects for efficient genetic improvement of reindeer and can be used in developing recommendations for selection practices in reindeer husbandry.

3 MATERIALS AND METHODS

3.1 INTERVIEWS

To investigate the demand for and practices of selective breeding and their regional differences in the reindeer-herding area in Finland, the managers of the reindeer-herding cooperatives (in Finnish *poroisäntä*, a total of 56) were interviewed for their views on selection and management (I–III). The questionnaire contained open and structured questions with the main themes as follows: i) background information of interviewee, ii) available resources and iii) selection criteria in practical reindeer husbandry. To compare the regional differences, the reindeer-herding area was divided into six regions, with the division following the borders of the marking districts (in Finnish *merkkipiiri*) to minimize intercooperative variation (Danell and Norberg 2010, III).

3.2 KUTUHARJU DATA

The Kutuharju experimental herd, in the village of Kaamanen, Inari, Finland (61°10'N), has unique detailed data on animals with production records and family information. The herd is owned and managed by the Reindeer Herders' Association, with data handling done in the Finnish Game and Fisheries Research Institute's Reindeer Research Station. Annually, the herd includes about 100 females and from 5 to 20 breeding males. The Kutuharju data were used for studying the factors affecting the variation in reindeer birth traits (IV), growth (V) and lifetime production (V). The data consisted of 2980 calves born in the herd in 1969–2011. The number of individual dams and sires are 566 and 101, respectively. Together with the imported animals, there were in total 3320 individuals in the pedigree.

The animals have been monitored regularly and records on individuals formed very detailed data suitable for genetic studies. The paternities were partially confirmed earlier with marking harnesses and since 1997 with DNA marker analyses at the Norwegian School of Veterinary Science (Røed *et al.* 2002). The data are divided into calf traits and dam traits.

CALF TRAITS

The calf traits studied were birth date (BD), birth weight (BW) (IV, V) and *growth* measured as average daily gain (ADG) (V) (Table 1). The calf's weight in the first autumn (AW1) was also used in the analyses (V).

BD was defined as days from 1st May (the first day of calving season). The last accepted date was 16th June to leave out the very-late-born calves.

Most of the calves were weighed in September (preferred record), occasionally in October or November (**IV**, **V**). ADG (g/day) was counted as (AW1-BW) / age at weighing (**V**).

Calves without information on sires were excluded from the data. Furthermore, calves without BD or BW were excluded from the data in **IV** and calves without ADG in **V**. There were 1136 and 1158 calves in the datasets in **IV** and **V**, respectively. The coefficient of variation (CV%) was moderate (about 15–25) in growth and weight traits, higher (37–51) in reproduction-related traits and very high in lifetime production traits.

DAM TRAITS

The dam traits studied were *age at maturity* and traits related to lifetime production (Table 1) (**V**). Age at maturity is measured as the age at first calving, in years. The profitability of meat production is highly influenced by the dams' herd life length and calving regularity. These could be measured by the dam's lifetime production expressed as individual fitness (λ_{ind}) or as *cumulative weaning weight of her calves over time* (here 7 years, WW7). The term λ_{ind} measures individual survival and reproduction over time and is based on individual Leslie matrices (Leslie 1945, 1948, McGraw and Caswell 1996), as applied in reindeer by Weladji *et al.* (2006). WW7, according to Martinez *et al.* (2004a), included the cumulative sum of the autumn weights of calves for each dam (**V**). The weights in WW7 were corrected for the birth year and sex of the calves.

The early predictors for the dam's lifetime production, such as her weight in the first autumn (as a calf) (DAW1), her average daily gain (D_ADG) in her first year (as a calf) and the autumn weight of her first calf (CAW1), are desirable indicator traits for efficient selection. The dam's adult weight in autumn prior to calving (DW) was used to study its relationship with her calf's BD and BW (**IV**).

There were 1165 females in the data, of which 600 were 1 year of age or older. Only the complete age cohorts were used in analysing the dam traits (*cf.* Tanida *et al.* 1988), therefore the birth years of the dams analysed were restricted to 1964–2000 in the respective data.

Table 1. *Numbers of animals, means, standard deviations (SD) and coefficient of variations (CV%) in birth date (BD), birth weight (BW), calf's autumn weight (AW1), dam's adult weight in autumn prior to calving (DW), age at maturity, individual fitness (λ_{ind}), cumulative weaning weights of calves over 7 years (WW7), dam weight in her first autumn (DAW1), average daily gain of female in her first year (as a calf) (D_ADG) and autumn weight of dam's first calf (CAW1).*

Trait	N	Mean	Min	Max	SD	CV%	Article
<i>Calf traits</i>							
Birth date, BD (days since 1 May)	984	18 May	2 May	16 June	7.8	37	IV
Birth weight, BW (kg)	984	6.1	1.8	10.4	0.89	15	IV, V
Calf autumn weight, AW1 (kg)	984	45.3	24	68	6.76	15	V
Average daily gain, ADG (g/day)	984	315.7	156	493	54.04	17	V
<i>Dam traits</i>							
Dam autumn weight prior to calving, DW (kg)	334	82	54	107	8.99	11	IV
Age at maturity (years)	575	3.1	1	7	1.58	51	V
Individual fitness, λ_{ind}	1165	0.46	0	1.62	0.58	127	V
Cumulative weaning weight of calves over 7 years, WW7 (kg)	1165	49.4	0	301	78.6	159	V
Dam weight in her first autumn, DAW1 (kg)	694	41.9	25	70	6.25	15	V
Average daily gain of female in her first year, D_ADG (g/day)	693	236	99	409	60	25	V
Autumn weight of dam's first calf, CAW1 (kg)	259	40.9	25	62	6.97	17	V

3.3 COOPERATIVE AND WEATHER DATA

The official statistics on the reindeer-herding cooperatives were used to assess a typical herd composition, selection intensity and intensity of predation (I–III). The statistics for each reindeer-herding year and cooperative are published in the second issue of each edition in Poromies (Paliskuntain yhdistys 2013).

Under extreme conditions, weather is an important factor explaining some of the annual variation in animals' performance. The weather was included in the statistical analyses (IV), using North Atlantic Oscillation (NAO) indices (Hurrell 1995). The NAO indices summarize the variation in weather conditions and are commonly used in phenological studies related to animals and plants (e.g. Weladji and Holand 2003). The monthly indices were obtained from the Climate Prediction Center Internet Team (2013).

3.4 METHODS

INTERVIEWS

The information gained from the interviews (in all 45) was saved with the survey software Webropol (Webropol 2010). The data obtained from the closed questions were analysed with statistical software R (R Development Core Team 2011). The differences among the regions were assessed, using analysis of variance (ANOVA), and the significance of the contrasts was tested with Scheffé's method (III). In addition, the differences between the regions were confirmed, using principal component analysis (PCA), carried out with the ade4 package in R (Dray and Dufour 2007, R Development Core Team 2011, III).

ESTIMATION OF GENETIC PARAMETERS

Fixed effects need to be taken into account to obtain accurate and unbiased estimates in genetic analyses (IV, V). The tested (F test) fixed effects were birth year, parity, sire age, sex and absence or presence of calf prior dam's pregnancy (IV, V). The annual variation in BW and BD, mostly caused by weather, was further studied, using regression analyses with monthly NAO indices (Hurrell 1995) (IV).

The (co)variance components were estimated using the restricted maximum likelihood (REML) method (Patterson and Thompson 1971) with an animal model (IV, V). Three different models were used for the calf traits: 1) direct genetic effect of the animal, 2) direct and maternal effects, and 3) direct and maternal effects and maternal permanent environmental effect. The dam traits were analysed, using the first model. The correlations between the traits were analysed with bivariate analyses (IV, V). The

significance of the random effects was tested with the likelihood ratio test (Pinheiro and Bates 2000).

The sire-maternal grandsire (S-MGS) model is equivalent to the animal direct-maternal effect model (e.g. Eaglen and Bijma 2009). The two models were used for the same data to quantify the correlation between the residuals of the direct and maternal effects in ADG (\mathbf{V}).

The preliminary analyses and statistical tests were carried out with statistical software SAS EG, version 4.2 (SAS Institute Inc, Cary, NC, USA) and with R, versions 2.15.1 and 3.0.1 (R Development Core Team 2010, 2013). The (co)variance component estimations were done, using ASReml, release 3.0 (Gilmour *et al.* 2009).

4 MAIN RESULTS

4.1 IMPORTANCE OF SELECTION AMONG MANAGEMENT PRACTICES

In the interviews, the response rate was 80.4% (45 out of 56 managers), with the highest rate in the southern and western parts of the reindeer-herding area (II, III). The most striking differences between the regions were in animal density, herd size per household and selection intensity (all highest in the north) and in predation (highest in the southeast) (III).

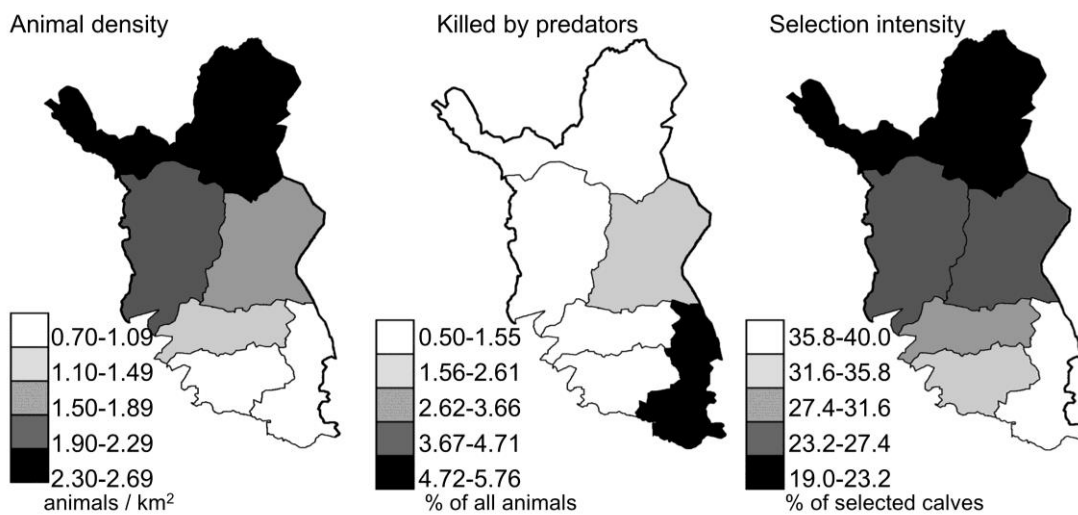


Figure 2 Regional differences in animal density, predation pressure and selection intensity among the six regions of the reindeer-herding area in Finland.

Independent of a region, managers regarded the selection of breeding animals as the most important among the factors affecting calf weight and survival (III). The managers listed the factors influencing the success of production in order of importance as follows:

1. Selection of breeding animals
2. Sufficient number of breeding males
3. Age distribution of females
4. Supplemental feeding
5. Number of predators
6. Quality of summer pastures
7. Weather in summer and insects
8. Herd size during summer and insects
9. Competing land use

The proportion of males in a cooperative ranged from 6.6% to 8.2% throughout the regions (III). Early calving, at 2 years of age, showed pros and cons: while it is beneficial to use all the reproductive capacity of the herd, early maturation is often considered to lead to poorer production in subsequent years (III).

The females are culled at ages of 10–12 years and the males at ages of 4–7 years (III). Managers state that the early culling of males is the main tool for guaranteeing fast turnover of breeding animals and for preventing inbreeding (III). Selection intensity varies throughout the regions, with the average proportion of selected calves being 29% of all calves (II).

There were regional differences in slaughter regime and feeding (III). Slaughter policy based on herder-specific quota is most common in the southern parts of the reindeer-herding area (III). Feeding is practiced overall, but is considered less important in the northernmost region (III). Book-keeping of individuals and animal identification are practiced by one-third of the managers and are most popular in the southwestern cooperatives (III). Of the managers, 58% are able to identify a dam among the majority of their individuals and over half use individual ear tags for their breeding animals.

4.2 SELECTION OBJECTIVES

The selection criteria in reindeer are related to calf phenotype and dam properties (II). Calf size and muscularity and dam traits guide the selection criteria, while managers do not consider antler traits, behaviour or colour of the calf as important (II). The selection criteria are, in order of importance, as follows (II):

1. Health
2. Vigour
3. Muscularity
4. Dam or dam line
5. Calf size
6. Dam's maternal care
7. Length and quality of hair
8. Early shedding of antler velvet
9. Branching antlers
10. Sharp or hard antler tips
11. Hair colour
12. Temperament
13. Suitability for sledge pulling or racing
14. Thick antler bases

There are no major regional differences in the main criteria, despite regional heterogeneity in production conditions (III). This means that regional differences, e.g. in the use of supplementary feeding, are not reflected in the selection criteria. Among the less important traits, antler traits are considered in the northern cooperatives, while suitability for racing is preferred in the southwestern region (III).

Managers have changed the selection criteria over the years, mostly in the southeastern region, where 85% of the managers have made changes within the last 5 years. The managers explained how they had to make compromises in the selection criteria, due to decreased numbers of selection candidates. Predation pressure has been highest in the same area (III).

4.3 GENETIC VARIATION IN THE TRAITS STUDIED

For the successful selection, there should be genetic variation in the targeted traits. To anticipate the outcome of selection, genetic variation can be estimated from data with production records and family information. The only reindeer data with individual and pedigree information are available in the Kutuharju experimental reindeer herd. This unique information gathered over the years allows extraction of genetic variation.

4.3.1 CALF TRAITS

The genetic analyses contained corrections for the fixed effects chosen. Of these effects, the year and parity most clearly affected all the traits, with the more experienced females having the earliest and heaviest calves. Furthermore, the male calves were heavier at birth, and the calves sired by the oldest males were born earlier and were also heavier in the autumn periods. Whether the dam had calf at foot prior to conception had no effect on calf traits. BD and BW were affected by the April and September NAOs of the previous year.

Of the random effects for BD and BW (IV) and ADG (V), the best fit was with the model containing animal and maternal effects. The heritability values, including Willham's and total heritability, and direct-maternal correlation values are presented in Table 2. Comparison of the animal's direct-maternal model with the S-MGS model revealed that the residuals of the direct and maternal effects were not correlated (V).

Table 2. *Willham's (h^2_w), direct (h^2_d), maternal (h^2_m) and total (T^2) heritabilities and direct-maternal genetic correlations (r_{am}) with standard errors in parentheses for birth date (BD), birth weight (BW) and average daily gain (ADG) of the calves born in the Kutuharju reindeer herd in 1987–2011.*

trait	h^2_w	h^2_d	h^2_m	r_{am}	T^2
BD	0.44	0.27 (0.09)	0.06 (0.05)	0.01 (0.54)	0.49
BW	0.73	0.23 (0.08)	0.24 (0.06)	0.17 (0.34)	0.61
ADG	0.10	0.24 (0.09)	0.18 (0.06)	-0.73 (0.17)	0.20

The h^2 estimates of BD and BW from the bivariate analyses were similar to those from the single-trait analyses (IV). The r_{am} in ADG was strongly negative (V), whereas in BW, BD, AW1 and DW the correlations were not significant. Of the intertrait correlations, ADG showed strong, positive correlation (direct genetic correlation $r_{g(d)}$, phenotypic correlation r_p and residual correlation r_e) with AW1 and negative correlations with BW ($r_{g(d)}$) and BD (maternal genetic correlation $r_{g(m)}$) (V). Of the other calf traits the only correlations larger than its standard error (SE) was the r_p between DW and BW (IV, V).

4.3.2 DAM TRAITS

In the single-trait analyses the h^2 estimate (SE) of age at maturity, λ_{ind} and WW7 was 0.07 (0.12), 0.10 (0.06) and 0.23 (0.07), respectively. In the bivariate context, the range of h^2 values and correlations between traits are presented in Table 3 (V). All the correlations except the one between age at maturity and λ_{ind} were positive.

Table 3. *Range of heritability (on the diagonal) and genetic (upper diagonal) and phenotypic (lower diagonal) correlations for the age at maturity, individual fitness (λ_{ind}) and cumulative weaning weights of calves over 7 years (WW7), dam's calf weight in her first year (DAW), her growth (D_ADG) and her first calf's autumn weight (CAW1) in the Kutuharju reindeer herd in 1964–2011.*

	Age at maturity	λ_{ind}	WW7	DAW	D_ADG	CAW1
Age at maturity	0.05–0.17 (0.12–0.13)		ns			ns
λ_{ind}	ns	0.07–0.13 (0.06–0.07)				ns
WW7	ns		0.22–0.30 (0.07)			
DAW	ns			0.49–0.58 (0.08–0.09)		
D_ADG	ns				0.15–0.19 (0.08)	ns
CAW1	ns					0.04–0.08 (0.10–0.16)

ns = nonsignificant

	0.01 < $ r_g $ < 0.25	0.25 < $ r_g $ < 0.50
	0.50 < $ r_g $ < 0.75	0.75 < $ r_g $

The results of the genetic correlations from the bivariate analyses could be summarized as follows: 1) the early-maturing animals showed high lifetime production, 2) traits expressing lifetime production were strongly correlated and 3) the dam's early traits (her own calf-time growth and her first calf's autumn weight) are good indicators for her lifetime production.

5 DISCUSSION

Understanding the feasibilities and consequences of genetic improvement of productivity is vital to reindeer herding. Riseth (2006) discussed the main driving factors for reindeer husbandry and argued that the primary motivation is not related to profit-making but to the herders' regard for their occupation as a way of life (*cf.* Mazzullo 2010). Modern herding is more market-oriented (Rönnegård 2003, I) and the economic return is needed for maintaining the livelihood of herders and infrastructure and resources of the husbandry system (Riseth 2000, I). The costs of feed and vehicles together with diminishing pasture areas encourage herders to focus on improving the economics of their operations and performance of individual animals (Danell 1999, I).

Reindeer herders share their pasture lands and carry out herding operations jointly (Riseth 2000, I). The cooperative system, however, leaves room for some owners to not follow selection guidelines, which leads to an overall lower genetic gain (Rönnegård *et al.* 2003). The effect of nonfollowers may be reduced if the breeding males are selected among the animals owned by the herders actively contributing to the selection (Rönnegård 2003).

The objectives of this thesis were to determine the current state of selection and to assess the potential for genetic improvement of reindeer meat production. To meet these objectives, we interviewed the managers of reindeer herding units, analysed the official statistics available on reindeer production and carried out genetic analyses of the calf and dam traits affecting meat production.

5.1 DATA AND METHODS

The managers are representatives of their cooperatives (Poronhoitolaki 1990, I) and the best informants in their area (II, III). They form a competent group and the combined results of the interview study gave a comprehensive picture of the reindeer husbandry in Finland. The high response rate indicated the managers' keen interest in improving the herding operations (II, III).

The interview results that were scaled from 0 to 3 were categorical and performing ANOVA with such data needs caution (III). Overall, the ANOVA approach was performed for all the data and it is beneficial to have the same analysis for all the traits for better comparison and consistency. To test the use of ANOVA, Kruskal-Wallis analyses were also conducted for the categorical traits. The results were very similar to those from ANOVA (III).

The Kutuharju data are unique in reindeer research, since they include information on sires and detailed records of individuals (IV, V). Reliable genetic estimates give an indication of the sufficiency of the data for the analyses. The power of the analysis would have benefited from more data. In comparison, analyses of red deer (*Cervus elaphus elaphus*) were carried out with 2000–3000 animals, with successful extraction of maternal effects (Kruuk and Hadfield 2007, Archer *et al.* 2013). In farmed livestock, datasets of 100 000 animals or more are commonly found (*e.g.* Meyer 1997, Eaglen and Bijma 2009). Due to the limited amount of data, the multivariate analyses were replaced with a set of bivariate analyses for the poorly heritable or weakly correlated traits. The variation due to the maternal permanent effect was likewise not significant. Possibly, a larger dataset could have aided in capturing the variation.

Here, lifetime production was measured as the cumulative sum of weaning weights by the age of 7 years (V). The cutting point was chosen as 7 years to provide sufficient amounts of data for the study and enable detection of the differences among the animals.

5.2 CURRENT STATE OF SELECTION

Reindeer husbandry has characteristics that must be taken into account in selection, particularly the semidomesticated nature of the livelihood, joint activities in many herding operations and joint use of resources (Rönnegård 2003). However, the current state of selection is encouraging: reindeer herders are very interested in selection and the criteria they use are sound and similar throughout the regions and with high selection intensity (II, III). This forms a very promising starting point for any suggestions for the improvement of selective breeding.

The main selection traits are related to meat production (*cf.* Danell 1999, II, III) and there is genetic variation in the traits (IV, V). As in red deer (McManus and Thompson 1993) and beef cattle (Phocas *et al.* 1998, Wolfová *et al.* 2005), empirical selection in reindeer favours heavy, muscular calves, while the dam's performance is also crucial to selection (II).

The main selection criteria are similar throughout the reindeer-herding area, despite the differences between regions (III). For example, feeding in the northernmost region is not as important as in the other regions (III). Similar criteria facilitate joint operations for genetic improvement, *e.g.* guidelines for breeding schemes regardless of the region or ethnicity of a herder.

The efficiency of selection is greatly dependent on the herder (*cf.* McManus and Thompson 1993). Weladji *et al.* (2002) reported differences between reindeer carcass weights among various owners in Norway. The ranking of animals for weight is based on subjective visual inspection of the animals in the autumn roundups (II). The benefit of a roundup is to have all

the calves together to enable the herder to compare them with the contemporary group (Falconer and Mackay 1997, **II**).

Selection intensity is dependent on the age at maturity and reproductive capacity (Falconer and Mackay 1997). Both are reflected in generation turnover and rate of genetic improvement. Selection intensity is high in the cooperatives (**III**). Selection efficiency is regionally affected by natural selection (mostly predation, **III**, Figure 2). Sharing of common resources in reindeer herding also affects selection intensity (Rönnegård and Danell 2003).

Selection should be considered jointly with the aims of optimizing the herd composition (Lenvik 1988, Danell 1999, Rönnegård 2003, Holand 2007). The proportions of prime-aged females are maximized and there is a small but sufficient number of males, as recommended for optimal performance (e.g. Lenvik 1988, Danell 1999, Holand 2007). However, the calves used for breeding purposes should not be selected from the oldest dams so as to accelerate genetic progress.

Selection may increase the risk of inbreeding. Herders actively prevent inbreeding by replacing breeding males regularly and exchanging them within and between the cooperatives (**III**). The number of progeny per sire cannot be controlled by herders (Rönnegård and Danell 2001), although the limited reproductive capacity of the male sets an annual limit. In the study by Røed *et al.* (2002), the best male sired 20 calves in 1 year. The only means for control would be by castration or culling of poorer or older males in autumn. Rönnegård *et al.* (2003) showed that inbreeding is not a problem in large (< 2000 animals) cooperatives.

5.3 GENETIC VARIATION

Meat production is dependent on several animal-related factors (Figure 3), particularly on the product of the weight and number of calves. The traits analysed are divided into calf and dam traits and show the results of genetic variation.

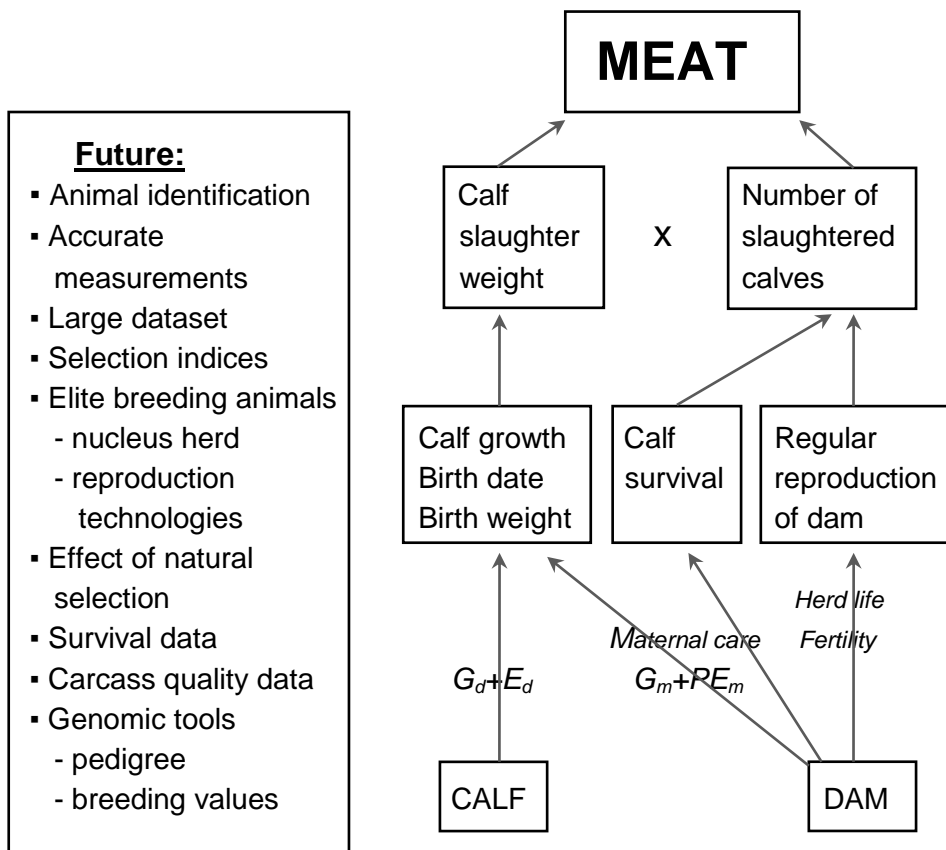


Figure 3 General scheme of the traits affecting meat production. Direct additive genetic effect G_d , additive maternal genetic effect G_m , animal's environmental effect E_d and maternal permanent environmental effect PE_m denote the genetic and environmental parts of the calf's direct and maternal effect. The "Future" column lists the challenges and opportunities foreseen in selective breeding.

CALF TRAITS

Calf weight is determined by several variables: the calf's birth date, birth weight and growth from birth to autumn (until slaughter). In addition to common heritability value, the amount of total genetic variation in the variables can be described as its evolvability (Houle 1992). The evolvability (CV_A) is expressed as the available total additive genetic variation in relation to the mean (Houle 1992, Bijma 2006) and quantifies the potential change by selection. The CV_A was from 5% to 9% for autumn weights and average daily gain of calf and dam, 10% for birth weight and 20% for birth date (IV). The evolvability values of the calf traits are comparable to the genetic changes expected in the selection schemes of economically important livestock traits expressed with respect to the mean (Smith, 1984).

In reindeer, the total heritability value of birth weight (0.61) was larger than in red deer (0.14–0.46) (McManus 1993, Clements *et al.* 2011). In birth date the total heritability value was 0.49, whereas in red deer the related conception date showed a heritability value of 0.2 (Archer *et al.* 2013). In calf

growth the total heritability values were similar to those estimated for autumn weight by Rönnegård and Danell (2003) but smaller than Varo's (1972) estimates obtained from small data. In farmed red deer, the weaning weight heritability values obtained among various farmed populations were larger, varying from 0.36 to 0.89 (McManus 1993).

The direct and maternal heritability values in reindeer (**IV**) are similar in birth weight and smaller in growth than in domestic sheep (Safari *et al.* 2005). Like the common finding in growth traits (Heydarpour *et al.* 2008), the maternal heritability value in growth of reindeer is smaller than that of direct heritability (**V**).

The herders select breeding individuals in terms of calf autumn weight (measured as calf size and muscularity) (*cf.* Danell 1999, **II**, **III**). Due to favourable genetic correlation, the selection of large calves in autumn leads to faster growth, heavier adult females and eventually to higher lifetime calf (meat) production (**V**). Similar results have been found in other species: in beef cattle (Bourdon and Brinks 1982, Morris *et al.* 1992), red deer (McManus 1993) and sheep (Safari *et al.* 2005).

The calf's live weight is phenotypically correlated with dressing percentage in reindeer (Petersson and Danell 1993) and genetically in red deer (McManus 1993) and in beef cattle (Morris *et al.* 1992). Favourable genetic correlation between live weight and muscularity, and live weight and carcass fatness are also found in sheep (review by Safari *et al.* 2005). In beef cattle, significant positive economic values for carcass conformation relative to growth rate were found (Phocas *et al.* 1998).

The calf autumn weight could also be considered as the optimum trait. The very largest male calves may face competition by older males and suffer from poor survival over winter under harsh environmental conditions (Helle *et al.* 1987, Danell 1999, **II**). Moreover, Vehviläinen *et al.* (2012) reviewed how the high emphasis on growth in selection may result in poor health and survival. Similarly, large calves at birth increase the incidence of calving difficulties (Morris *et al.* 1992; Eaglen and Bijma 2009). Most reindeer dams give birth in the wild and information on calving difficulties is lacking. The birth weight is heritable (**IV**, **V**) and may in wild ungulates be phenotypically associated with good survival (Gaillard *et al.* 2002b).

DAM TRAITS

The reindeer dam is crucial to the efficiency of meat production (Danell 1999, Rönnegård 2003, Holand 2007). Production is maximized when females mature early, calve regularly and maintain performance until old age. The dam's maternal care is also important for calves' growth (Weladji *et al.* 2006).

The Kutuharju data for dam traits were rather ineffective at detecting the low heritability values, typical of fitness-related traits (Bourdon and Brinks 1982, Falconer and Mackay 1997). On the other hand, the traits showed high evolvability (**V**, Table 1), also typical of fitness traits (Houle 1992). For age at

maturity the evolvability is 11%. The heritability estimates for age at maturity are small and with high standard errors (V). The early maturation of females is related to large body size, good condition and favourable environment (Gaillard *et al.* 2000b, Weladji *et al.* 2008).

The heritability value of individual fitness was low (V), possibly due to use of a coarse-grained scale. In the other lifetime measurement, cumulative weaning weight, the heritability estimates found (0.22–0.30) were larger than those (0.17–0.13) in individual fitness and those (0.15–0.16) in beef cattle (Martinez *et al.* 2004a, 2004b) and domestic sheep (0.07–0.13) (Safari *et al.* 2005). Possibly, additional data with more females having records of lifetime performance would have improved the statistical power of the analysis (*cf.* Martinez *et al.* 2004b).

INDICATOR TRAITS AND DIRECT-MATERNAL CORRELATION

The traits related to the dam's lifetime productivity can be measured only late in her life. Indicator traits aid in selecting for such traits. Lifetime productivity is related to the dam's live weight as a calf and her age at maturity (V). In roe deer (*Capreolus capreolus*) and bighorn sheep (*Ovis canadensis*) the heavy adult weight coincides with high individual long-term fitness (Gaillard *et al.* 2000a).

The correlation between direct and maternal effects in a calf's performance is of concern in reindeer (Danell 1999, Holand 2007). The origin of strongly negative direct-maternal correlation in weight-related traits has been widely discussed (*cf.* Bijma 2006). In this study, the lack of dam information (Heydarpour *et al.* 2008) or the correlated residuals (Bijma 2006, Eaglen and Bijma 2009) did not affect the level of direct-maternal correlation. This may be due to the general allocation of metabolic resources (*e.g.* review by Heino and Kaitala 1999), which in reindeer can cause poor investment in maternal ability after high investment in growth. The negative correlation between dam weight and low protein content in milk was also discovered by Varo and Varo (1970).

Both direct and maternal effects need to be included in selection. Including dam traits in the selection criteria restricts the possible decline in maternal abilities when selecting for calf growth or weight (Danell 1999, Holand 2007).

6 OPPORTUNITIES AND CHALLENGES

Reindeer husbandry is in a process of transition (Riseth 2000), with the traditional livelihood adapting to new situations (I). On one hand, reindeer production faces challenges such as degraded and fragmented pastures and related need for supplementary feeding, predation, and climate warming with changing environmental conditions (I). On the other hand, reindeer meat has a positive image as an ethically produced and tasty product, with production being almost free of subsidies (I). Herders greatly value their way of life, are willing to adopt new ideas to ease their labour, and have a healthy tradition of working together (Riseth 2000, Mazzullo 2010, I). During recent decades, reindeer husbandry has undergone a technological revolution (Riseth 2000, I), suggesting that herders are willing to adopt new technologies that help to ease their labour or cut their expenses (I).

From the genetic point of view, there are clearly prospects for selection, although the practical aspects need to be resolved before these ideas can be realized (Figure 3). The challenges are related to animal identification, individual weighing, paternity determination, organization of data collection and exploiting new technology, e.g. genomics.

Modern DNA technologies assist in determining the paternities in reindeer (Røed *et al.* 2002). Due to their high reproductive capacity, the sires are the most influential for the success of selection. The genetic quality of sires can be determined, using the records from their offspring. Information on paternities enables the unbiased and accurate estimation of breeding values for the sires and all the animals (Falconer and Mackay 1997). It is only with the information on sires that the maternal effects could be estimated (IV).

A modern tool related to DNA technologies and phenotypic data is genomic selection (see review on exploitation of genomics by Mäki-Tanila 2012). Large and detailed datasets could be used as a reference population for genomic selection. In genomic analysis, a hair sample or nasal swab is sufficient for DNA typing to be integrated with traditional and modern ways of collecting and itemizing useful information from the reindeer. The pedigree could be formed, using DNA information, and with this type of closed breeding population the genomic analysis should function without complications (Mäki-Tanila 2012). The costs in DNA analyses and, hence, in establishing a breeding programme based on genomic selection are also decreasing very rapidly. The more complete pedigree, gained with DNA analyses, aids in controlling the rate of inbreeding and possible losses of genetic variation, which is important in animal breeding (Flint and Woolliams 2008). Predation may increase the risk of inbreeding and therefore genetic diversity in the population is needed to decipher the risks of inbreeding in the changing environment.

No planned or controlled use of breeding males occurs in reindeer husbandry. The animals roam free in the wild with no human interference in mating of breeding animals. However, artificial insemination (Dott and Utsi 1973) and embryo transfer (Lindeberg and Valtonen 1999) have undergone trials in reindeer. Reproduction technology could be a useful future tool for elite breeding animals, as is already done with farmed livestock (Smith 1984). Herders could be encouraged to invest in superior animals if the genetic gain were estimated directly in monetary value (euro value for the offspring of an elite sire compared with the calf representing the herd mean). However, it is crucial to remember the specialities of the livelihood – the image of reindeer herding relies on natural resources and sustainable production (I).

The natural image is an essential part of reindeer meat production and should be exploited in the marketing of reindeer meat. Traditional reindeer meat products have been approved in the specified European Union (EU) quality scheme, “Protected Designation of Origin” (Council Regulation (EC) No 510/2006). In addition, reindeer husbandry is superior in terms of cultural values, animal welfare and feeding on pasture resources. Most of the meat originates from animals that are not fed but live free in the northern wilderness, regarded as a genuinely clean environment (I). Since the reindeer is an icon animal of Lapland with a small production volume, the meat is regarded as a northern delicacy with an ethical, healthy image (*cf.* Hoffman and Wiklund 2006, I). Therefore, it may be risky to suggest elaborate technologies that could alter the image of reindeer, and their use should be preceded by open discussion of the advantages.

Organized data collection is a basic requirement for any type of development scheme in animal production. Animal identification is the first step needed for effective selective breeding in reindeer, particularly in dam productivity (Danell 1999, Rönnegård 2003). Book-keeping of animals and individual ear tags are already commonly used among herders and there are good empirical means for animal identification (Lenvik 1988, III). As many as half of the managers use individual ear tags for their animals, while identification collars are also used in many cooperatives (II).

Objective weight measurements would be more accurate and better reveal the genetic differences available among selection candidates (Danell 1999, Rönnegård 2003). The challenge in weighing the animals is the hectic roundup with little time or work budget for additional tasks such as weighing. Therefore, the benefits gained by any additional work should be demonstrated well before proposing the adoption of new technologies in reindeer herding (*cf.* Rönnegård 2003). Favourable experiences in Sweden (Rönnegård 2003) and in Norway (Lenvik 1988, Riseth 2000) show that it is possible to include weighing among the roundup activities. Furthermore, with electronic (or bar-code) identification and automatic scales, accurate measurements could be obtained without slow manual weighing and disturbing the smooth performance of the roundups.

The identification, production recording and pedigree information from many cooperatives could form a joint large dataset of animals and their pedigrees throughout the herding units. These types of data would enable the assessment of selection schemes for the breeding objectives, choice of selection indices with economic weights and finally the estimation of breeding values for individuals, including also the maternal component (McManus and Thompson 1993, Goddard 1998, Wolfová *et al.* 2005). A breeding scheme based on accurate breeding values of all relevant traits is the best tool for genetic improvement in animals. If electronic identification is used, a list of real-time breeding values could be immediately available when the animals arrive in the roundup.

A large dataset with information on thousands of animals could also be the way to solve the challenge due to the antagonistic correlation between direct and maternal effects. Among very numerous animals, those with the least negative or even positive direct and maternal genetic effects could be detected and selected for breeding. A reasonable correlation of residuals of direct and maternal effects could also be estimated from a sufficiently large dataset (*cf.* Eaglen and Bijma, 2009).

The maternal effects in the analyses are included in a wider concept of indirect genetic effects. Among these the social interactions, particularly competition among individuals for limited resources, may alter the response to selection (Bijma 2014, Wilson 2014). The maternal effect is a good example of social interactions. In addition, the high social rank of a female in the herd may improve the calf's preweaning growth (Holand *et al.* 2004). To study the effect of this type of social interaction in reindeer, there is a need to collect the appropriate data and to consider including the information in selection.

Calf survival directly affects the number of calves slaughtered. Survival is a categorical trait that, in extreme proportions, is rather challenging for genetic analyses (Gaillard *et al.* 2000b). In Kutuharju, about 20% of the calves are lost before the autumn roundup, and with the rather moderate amount of data available it was not possible to obtain heritability estimates for the trait. A large dataset with information including the causes of death (e.g. using mortality radio transmitters attached to collars, as described in Norberg *et al.* 2006) could help to quantify the heritability value in survival. The genotype-environment (GxE) interaction (Strandberg 2012) in all the traits could also be studied with the aid of a large dataset. Some herders found that imported calves have poor survival (likely due to nongenetic factors, such as differences in feed and microbial environment) and this phenomenon needs further research. In addition to the practical research question, the productivity of given genotypes over a whole range of environments are of interest. Again, larger datasets would be valuable in quantifying the GxE interaction.

Management is important in reindeer husbandry and selective breeding could be integrated with it. For example, feeding improves calf production

and calf growth (Kumpula *et al.* 2002) and provides a good framework for selection, since the animals are under better control with less exposure to natural selection (III). Better control could also protect the animals from predation (I). Currently, predation is among the main challenges in reindeer husbandry (I). Predation pressure has increased considerably during recent decades (Danell and Norberg 2010, Paliskuntain yhdistys 2013) and has resulted in places in drastically reduced feasibilities for selection (Fig. 3, III).

Natural selection plays an important role in reindeer husbandry. Danell (1999) discussed how selection based on growth may lead to the need for an improved environment (*cf.* Helle *et al.* 1987). Changing environmental conditions induce challenges in establishing an efficient breeding scheme (Holand 2007). In the long run, the supplementally fed reindeer may begin to differentiate from those living on natural pastures.

Carcass quality has been successfully measured in Sweden (Olofsson 2011). In Finland there is no classification for differentiated pricing, such as the EUROP, of reindeer carcasses in slaughterhouses to pay incentives for high quality and to collect information. It would be beneficial to determine the place of carcass quality in breeding objectives and its genetic variation and selection potential.

An efficient use of elite breeding animals would improve the prospects for selection (Varo 1972). Similar selection criteria throughout the area would strengthen first the feasibilities of exchanging breeding animals between cooperatives, or further the idea of establishing a joint scheme based on a nucleus herd (*cf.* Rönnegård 2003). A nucleus herd, open or closed, would be a cost-efficient tool for genetic improvement (Rönnegård *et al.* 2003).

In conclusion, the development of genetic improvement in reindeer should be done step by step. Before any selection is feasible, it is essential to have a system for animal identification, sire ascertainment and a pedigree database. Most of the pedigree construction is based on wide-scale DNA marker genotyping.

The next step is to organize the collection of phenotypic records of calvings and calf autumn weight. Combined with the pedigree information, this would facilitate genetic evaluation. Ideally, the genetic ranking of animals would be available at the roundups as soon as the phenotypic records are measured. Information for the improvement of meat production traits should include data on carcass quality, which could be merged together with other information from the animals. The carcass quality data are collected in collaboration with slaughterhouses.

An effective genetic improvement scheme would require a population of at least several thousand females. To obtain satisfactory improvement throughout the reindeer-herding area, there should be perhaps several such schemes covering different regions. Selection produces permanent changes with fairly small investments and offers a cost-efficient way to improve the profitability of production. Efficient selection assists in keeping the reindeer running in the roundup corrals.

REFERENCES

- Anttonen, M., Kumpula, J. and Colpaert, A. 2011. Range selection by semi-domesticated reindeer (*Rangifer tarandus tarandus*) in relation to infrastructure and human activity in the boreal forest environment, Northern Finland. *Arctic* 64: 1-14.
- Archer, J.A., Asher, G.W., Fisher, P.J., Ward, J.F., Scott, I.C., Bixley, M.J., Hickey, S.M. & Morris, C.A. 2013. Genetics of early concpetion and its relationship to growth traits in red deer (*Cervus elaphus*). *Animal Production Science* 53: 1083-1087.
- Bijma, P. 2006. Estimating maternal genetic effects in livestock. *Journal of Animal Science* 84: 800-806.
- Bijma, P. 2014. The quantitative genetics of indirect genetic effects: a selective review of modelling issues. *Heredity* 112: 61-69.
- Bourdon, R.M and Brinks, J.S. 1982. Genetic, environmental and phenotypic relationships among gestation length, birth weight, growth traits and age at first calving in beef cattle. *Journal of Animal Science* 55: 543-553.
- Clements, M.N., Clutton-Brock, T.H., Guinness, F.E., Pemberton, J.M. and Kruuk, L.E.B. 2011. Variances and covariances of phenological traits in a wild mammal population. *Evolution* 65: 788-801.
- Climate Prediction Center Internet Team 2013. North Atlantic Oscillation (NAO). Cited Jan 12, 2013. Available from: <http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml>.
- Council Regulation (EC) No 510/2006 of 20 March 2006 on the protection of geographical indications and designations of origin for agricultural products and foodstuffs.
- Danell, Ö. 1999. Optimal produktion. *Rangifer* 19: 125-135.
- Danell, Ö. and Norberg, H. 2010. Petoeläintilanteen ja liikennevahinkojen vaikutukset Suomen poromääriin vuosina 2005/2006-2008/2009 [The effects of the carnivore population and animal deaths in traffic on the slaughter quantities in the period 2005/2006-2008/2009; predator and traffic damages]. *Poromies* 77 (6/2010): 15-21.
- Dray, S. and Dufour, A. 2007. The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software* 22: 1-20.
- Dott, H.M. and Utsi, M.N.P. 1973. Artificial insemination of reindeer (*Rangifer tarandus*). *Journal of Zoology* 170: 505–508.
- Eaglen, S.A.E. and Bijma, P. 2009. Genetic parameters of direct and maternal effects for calving ease in Dutch Holstein-Friesian cattle. *Journal of Dairy Science* 92: 2229-2237.
- Falconer, D.S. 1965. Maternal effects and selection response. In: Geerts, S.J. (ed): *Genetics today*. Pergamon press, New York.
- Falconer, D.S. and Mackay, T.F.C. 1997. *Introduction to quantitative genetics*. Fourth ed. 464 p.
- Flint, A.P.F. and Woolliams, J.A. 2008. Precision animal breeding. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363: 573-590.
- Gaillard, J-M., Festa-Bianchet, M., Delorme, D. and Jorgenson, J.T. 2000a. Body mass and individual fitness in female ungulates: bigger is not

- always better. *Proceedings of the Royal Society B: Biological Sciences* 267: 471-477.
- Gaillard, J-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. and Toigo, C. 2000b. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31: 367-393.
- Gilmour, A.R., Gogel, B.J., Cullis, B.R. and Thompson, R. 2009. ASReml user guide. Release 3.0. VSN International Ltd, Hemel Hempstead, HP1 1 ES, UK. www.vsn.co.uk.
- Goddard, M.E. 1998. Consensus and debate in the definition of breeding objectives. *Journal of Dairy Science* 81: 6-18.
- Heino, P. and Kaitala, V. 1999. Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *Journal of Evolutionary Biology* 12: 423-429.
- Helle, T., Pulliainen, E. and Aspi, J. 1987. Size-related changes in winter condition of male calves in reindeer. *Rangifer* 7: 2-11.
- Heydarpour, M., Schaeffer, L.R. and Yazdi, M.H. 2008. Influence of population structure on estimates of direct and maternal parameters. *Journal of Animal Breeding and Genetics* 125: 89-99.
- Hoffman, L.C. and Wiklund, E. 2006. Game and venison – meat for the modern consumer. *Meat Science* 74: 197-208.
- Holand, Ø. 2007. Flokkstruktur og slaktestrategi i reindrifta – et historisk perspektiv [Herd composition and slaughtering strategy in reindeer husbandry – revisited]. *Rangifer Report no. 12*: 21-33.
- Holand, Ø., Weladji, R.B., Gjølstein, H., Kumpula, J., Smith, M., Nieminen, M. and Røed, K.H. 2004. Reproductive effort in relation to maternal social rank in reindeer (*Rangifer tarandus*). *Behavioral Ecology and Sociobiology* 57: 69-76.
- Houle, D. 1992. Comparing evolvability and variability of quantitative traits. *Genetics* 130: 195-204.
- Hurrell, J.W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science* 269: 676-678.
- Ingold, T. 1978. The rationalization of reindeer management among Finnish Lapps. *Development and Change* 9: 103-132.
- Koerhuis, A.N.M. and Thompson, R. 1997. Models to estimate maternal effects for juvenile body weight in broiler chickens. *Genetics Selection Evolution* 29: 225-249.
- Kruuk, L.E.B. and Hadfield, J.D. 2007. How to separate genetic and environmental causes of similarity between relatives. *Journal of Evolutionary Biology* 20: 1890-1903.
- Kumpula, J., Colpaert, A. and Nieminen, M. 2002. Productivity factors of the Finnish semi-domesticated reindeer (*Rangifer t. tarandus*) stock during the 1990s. *Rangifer* 22: 3-12.
- Kumpula, J., Tanskanen, A., Colpaert, A., Anttonen, M., Törmänen, H., Siitari, J. and Siitari, S. 2009. Winter pastures in the northern part of reindeer management area in Finland during 2005-2008 - changes on the state of pastures after the mid of 1990s. *Riista- ja kalatalous - Tutkimuksia* 3/2009.
- Lenvik, D. 1988. Utvalgsstrategi i reinflokken. [Selection strategy in domestic reindeer]. Doctoral thesis. Reindriftsadministrasjonen, Alta.
- Leslie, P.H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33: 183-212.

- Leslie, P.H. 1948. Some further notes on the use of matrices in population mathematics. *Biometrika* 35: 213-245.
- Lindeberg, H. and Valtonen, M. 1999. Utilization of embryo transfer and in vitro production techniques for assisted reproduction in two multiparous species: The blue fox (*Alopex lagopus*) and European polecat (*Mustela putorius*) and in uniparous semi-domesticated reindeer (*Rangifer tarandus tarandus*). *Nordisk Jordbruksforskning* 81, p. 325. [21. NJF Congress: Agriculture and Society, Aas (Norway), 28 June – 1 July 1999.
- Lundqvist, H., Norell, L. and Danell, Ö. 2009. Relationships between biotic and abiotic range characteristics and productivity of reindeer husbandry in Sweden. *Rangifer* 29: 1-24.
- Martinez, G.E., Koch, R.M., Cundiff, L.V., Gregory, K.E. and Van Vleck, L.D. 2004a. Genetic parameters for six measures of length of productive life and three measures of life-time production by 6 yr after first calving for Hereford cows. *Journal of Animal Science* 82: 1912-1918.
- Martinez, G.E., Koch, R.M., Cundiff, L.V., Gregory, K.E. and Van Vleck, L.D. 2004b. Number of calves born, number of calves weaned, and cumulative weaning weight as measures of lifetime production for Hereford cows. *Journal of Animal Science* 82: 1903-1911.
- Mazzullo, N. 2010. More than meat on the hoof? Social significance of reindeer among Finnish Saami in a rationalized pastoralist economy. In: Stammler, F.M. and Takakura, H. (eds.) *Good to Eat, Good to Live With: Nomads and Animals in Northern Eurasia and Africa*. Sendai: Center for Northeast Asian Studies, Tohoku University. p. 101-119.
- McGraw, J.B. and Caswell, H. 1996. Estimation of individual fitness from life-history data. *The American Naturalist* 147: 47-64.
- McManus, C. 1993. Within-farm estimates of genetic and phenotypic parameters for growth and reproductive traits for red deer. *Animal Production* 57: 153-159.
- McManus, C. and Thompson, R. 1993. Breeding objectives for red deer. *Animal Production* 57: 161-167.
- Meyer, K. 1992. Bias and sampling covariances of estimates of variance components due to maternal effects. *Genetics, Selection, Evolution*: 24: 487-509.
- Meyer, K. 1997. Estimates of genetic parameters for weaning weight of beef cattle accounting for direct-maternal environmental covariances. *Livestock Production Science* 52: 187-199.
- Morris, C.A., Baker, R.L. and Hunter, J.C. 1992. Correlated responses to selection for yearling or 18-month weight in Angus and Hereford cattle. *Livestock Production Science* 30: 33-52.
- Mäki-Tanila, A. 2012. Animal molecular genetics from major genes to genomics. In: Meyers, R.A. (Ed.) *Encyclopedia of Sustainability Science and Technology*. pp. 463-472.
- Norberg, H., Kojola, I., Aikio, P. and Nylund, M. 2006. Predation by golden eagle *Aquila chrysaetos* on semi-domesticated reindeer *Rangifer tarandus* calves in northeastern Finnish Lapland. *Wildlife Biology* 12: 393-402.
- Olofsson, A. 2011. Towards adaptive management of reindeer grazing resources. Doctoral thesis, Sveriges lantbruksuniversitet. *Acta Universitatis Agriculturae Sueciae* 2011:16.
- Paliskuntain yhdistys 2013. Tilastoja poronhoitovuodelta 2011-2012 [Statistics on reindeer herding year 2011-2012]. *Poromies* 80, 2 / 2013: 30-37.

- Patterson, H.D. and Thompson, R. 1971. Recovery of inter-block information when block sizes are unequal. *Biometrika* 58: 545-554.
- Petersson, C.J. and Danell, B. 1993. Causes of variation in growth rate of reindeer calves. *Rangifer* 13: 105-116.
- Phocas, F., Bloch, C., Chapelle, P., Becherel, F., Renand, G. and Menissier, F. 1998. Developing a breeding objective for a French purebred beef cattle selection programme. *Livestock Production Science* 57: 49-65.
- Pinheiro, J.C. and Bates, D.M. 2000. Mixed effects models in S and S-PLUS. Springer Verlag.
- Poronhoitolaki 1990. Poronhoitolaki 14.9.1990/848 [Reindeer husbandry act].
- R Development Core Team 2010, 2011 and 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rantamäki-Lahtinen, L. (ed.) 2008. Porotalouden taloudelliset menestystekijät [Economic success factors of the reindeer husbandry]. MTT:n selvityksiä 156.
- Riseth, J.Å. 2000. Sámi reindeer management under technological change 1960-1990: Implications for common-pool resource use under various natural and institutional conditions. PhD thesis. Agricultural University of Norway.
- Riseth, J.Å. 2006. Sami reindeer herd managers: why do they stay in a low-profit business? *British Food Journal* 108: 541-559.
- Røed, K.H. 2005. Refugial origin and postglacial colonization of holarctic reindeer and caribou. *Rangifer* 25: 19-30.
- Røed, K.H., Holand, Ø., Smith, M.E., Gjølstein, H., Kumpula, J. and Nieminen, M. 2002. Reproductive success in reindeer males in a herd with varying sex ratio. *Molecular Ecology* 11: 1239-1243.
- Rönnegård, L. 2003. Selection, maternal effects and inbreeding in reindeer husbandry. Doctoral thesis, Sveriges lantbruksuniversitet. *Acta Universitatis agriculturae Sueciae*.
- Rönnegård, L. and Danell, Ö. 2001. Gene flow and potential selection response in age-structured subpopulations having a common male pool. *Animal Science* 72: 427-440.
- Rönnegård, L. and Danell, Ö. 2003. Genetic response to selection on reindeer calf weights. *Rangifer* 23: 13-20.
- Rönnegård, L., Woolliams, J.A. and Danell, Ö. 2003. Breeding schemes in reindeer husbandry. *Rangifer* 23: 45-57.
- Safari, E., Fogarty, N.M. and Gilmour, A.R. 2005. A review of genetic parameter estimates for wool, growth, meat and reproduction traits in sheep. *Livestock Production Science* 92: 271-289.
- Smith, C. 1984. Rates of genetic change in farm livestock. *Research and Development in Agriculture* 79:1482-1488.
- Strandberg, E. 2012. Animal genetic in environment interaction. In: Meyers, R.A. (Ed.) *Encyclopedia of Sustainability Science and Technology*. pp. 463-472.
- Tanida, H., Hohenboken, W.D. and DeNise, S.K. 1988. Genetic Aspects of Longevity in Angus and Hereford Cows. *Journal of Animal Science* 66: 640-647.
- Tike, Maa- ja metsätalousministeriön tietopalvelukeskus. 2012. Maataloustilastot 2012. [Agricultural statistics]. Cited 7 Nov, 2012. Available from: <http://www.maataloustilastot.fi>.

- Varo, M. 1972. Investigations on the possibilities of reindeer breeding II. Journal of the Scientific Agricultural Society of Finland 44: 234-248.
- Varo, M. and Varo, H. 1970. The milk production of reindeer cows and the share of milk in the growth of reindeer calves. Journal of the Scientific Agricultural Society of Finland 43: 1-10.
- Vehviläinen, H., Kauser, A., Kuukka-Anttila, H., Koskinen, H. and Paananen, T. 2012. Untangling the positive genetic correlation between rainbow trout growth and survival. Evolutionary Applications 5: 732-745.
- Webropol 2010. Online survey and analysis software. Available from: <http://w3.webropol.com/finland>
- Weladji, R.B., Gaillard, J-M., Yoccoz, N.G., Holand, Ø., Mysterud, A., Loison, A., Nieminen, M. and Stenseth, N.C. 2006. Good reindeer mothers live longer and become better in raising offspring. Proceedings of the Royal Society B: Biological Sciences 273: 1239-1244.
- Weladji R.B. and Holand, Ø. 2003. Global climate change and reindeer: effects of winter weather on the autumn weight and growth of calves. Oecologia 136: 317-323.
- Weladji R.B., Holand, Ø., Steinheim, G and Hansen, H. 2002. Effect of "owners" selection strategies on autumn weight in reindeer (*Rangifer t. tarandus*) calves. Rangifer 22: 107-113.
- Weladji, R.B., Loison, A., Gaillard, J-M., Holand, Ø., Mysterud, A., Yoccoz, N.G., Nieminen, M., Stenseth, N.C. and Ylönen, H. 2008. Heterogeneity in individual quality overrides costs of reproduction in female reindeer. Oecologia 156: 237-247.
- Willham, R.L. 1963. The covariance between relatives for characters composed of components contributed by related individuals. Biometrics 19: 18-27.
- Willham, R.L. 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. Journal of Animal Science 35: 1288-1293.
- Wilson, A.J. 2014. Competition as a source of constraint on life history evolution in natural populations. Heredity 112: 70-78.
- Wolfová, M., Wolf, J.B., Zahrádková, R., Přibyl, J., Daňo, J., Krupa, E. and Kíca, J. 2005. Breeding objectives for beef cattle used in different production systems: 2. Model application to production systems with the Charolais breed. Livestock Production Science 95: 217-230.